Population dynamics of seals: the influences of spatial and temporal structure

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Academic dissertation

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II Harding, KC. and Härkönen, T. (1999). Development in the Baltic grey seal *(Halichoerus grypus)* and ringed seal *(Phoca hispida)* populations during the 20 th century. — *Ambio 28:619-627.*

III Härkönen T., Harding K.C. and Lunneryd S.G. (1999). Age- and sex-specific behaviour in harbour seals *(Phoca vitulina)* leads to biased estimates of vital population parameters. — *J. Appl. Ecol. 36:825-841*.

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Abstract

This thesis explores how knowledge about temporal and spatial distribution, fecundity, mortality and age structure makes it possible to better understand the population dynamics of seals. Population growth rate and population size are the results of many internal population characters, such as age specific fertility and mortality rates. These internal population characters are influenced by external factors, such as fluxes in food availability and diseases. One example of life history plasticity is described for the Antarctic crabeater seal (Lobodon carcinophagus), where the mean age at sexual maturity increased significantly during 15 years (I). The observed delay in the age at sexual maturity together with information on age structure variations in the crabeater seals suggest that this population is regulated by a variable food supply. Environmental toxins and hunting are other external factors, affecting population growth by decreased fertility and increased mortality. The declines of the Baltic ringed seal (Phoca hispida) and grey seal (Halichoerus grypus) populations, from >190 000 and >88 000, respectively, to 4 000 -5 000 within 60 years (II), illustrate the impact such anthropogenic suppression can have.

Seal populations are structured into sex- and age-classes. The segregational behaviour of these groups leads to systematically skewed compositions of seals hauled out on land throughout the summer season, also if the true age structure is stable (III). This behavioural feature in combination with non-stable age structure was shown to produce biases in estimated population sizes of harbour seal (Phoca vitulina) ranging between +6 to -16 % (III). Further, harbour seals of different sex and age have different migration patterns (IV). Adult females show stronger site fidelity compared to all other population segments. These differences produce different age and sex compositions of nearby colonies. Thus, the spatial scale at which a seal population is observed adds another source of variation to estimates of population growth rate and other vital population parameters (IV).

Diseases can dramatically influence the population dynamics of seals as exemplified by the 1988 Phocine Distemper Virus (PDV) epizootic, when 55-60% of the total population succumbed to the disease. Regional differences in mortality patterns coincided with the temporal and spatial behaviour of seals at the time of infection (V). For example, colonies infected during early spring had high mortality of adult females whereas, at colonies infected late in the summer mostly adult males died. The following ten years of population growth in harbour seals exhibited conspicuous regional fluxes that are correlated to the regional skews in age distribution of the survivors of the epizootic (V).

Fine-scale information about spatial and temporal structure of populations can be crucial for the identification of the vital processes that govern the population dynamics of seals.

Introduction

Which factors determine the population dynamics of the long-lived, slowly reproducing seals? How much of the observed spatial and temporal variation in population growth is caused by external factors and sampling biases and how much can be derived from intrinsic population processes? In order to sort this out; let us simplify the processes that affect seal population dynamics as follows. Environmental factors such as; food availability, toxins and infectious diseases affect the life of individual seals. The response (in fecundity, mortality or migration patterns) of individuals to a given change in an external factor depends on the phenotypic plasticity of the individuals (Stearns and Koella 1986). The resulting life history responses of all individuals will set the population composition (e.g., age structure). The frequency and number of individuals with different character values of the life history features will in turn determine the population growth rate and population size (Caswell 1989). In populations where intra specific competition occur (e.g. due to food- or mate competition) population size can act as a regulating factor in itself, and thereby the population dynamic circle is closed. The vital population dynamic processes are summarised in Fig. 1.

The 'population dynamic circle' (fig. 1) also illustrates factors, which could be difficult to parameterise and thereby make the task to evaluate population growth trends problematic. In order to understand dynamics of real world populations we first need to understand the significance of various internal processes taking place in the focal population. In this process detailed data on the population growth trend, fecundity, mortality and migration rates, temporal and spatial population compositions are essential. Only after the internal processes are known it is possible to estimate the importance of external influences on seal populations. In the following I shall describe the life history of the seal species which are investigated in this thesis. Thereafter, major external factors that are known to influence the population dynamics of seals are reviewed. Finally the major results of this thesis are presented and discussed in relation to population regulating mechanisms.

General life-history features of phocid seals

The four species included in this thesis, the crabeater seal *(Lobodon carcinophagus)*, the grey seal *(Halichoerus grypus)*, the ringed seal *(Phoca hispida)* and the harbour seal *(Phoca vitulina)* all belong to the family of true seals (Phocidae). In general, the described species have maximum life spans of approximately 30-40 years. Females give birth to their first pup between 4 and 7 years of age and give, on average, birth to less than one pup annually. The mortality rate is highest during the first year of life

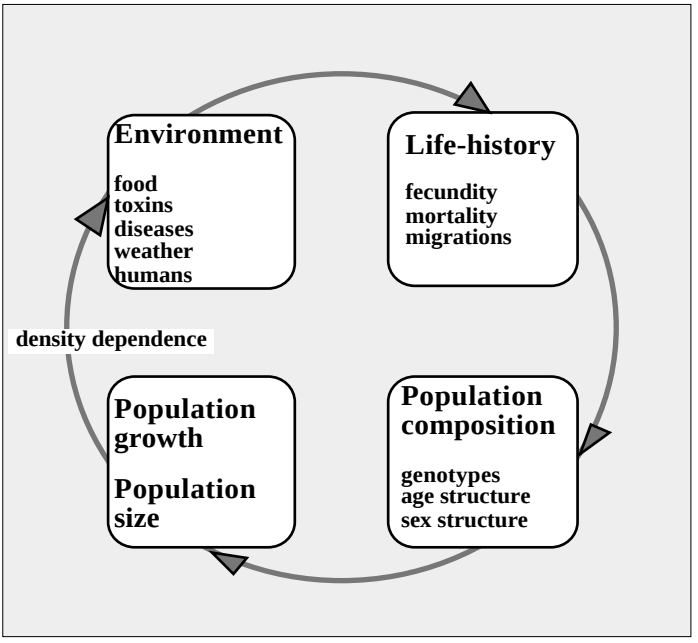

Fig. 1. *The 'population dynamic circle'. Schematic representation on how growth rate and size of a seal population are determined by the combined effects of external and internal factors. The arrows indicate the direction of the 'impact route'.*

(20-50 %), but levels off such that adult seals have annual mortality rates close to (4 - 10%). The life history characters of seals are often state dependent, viz., animals of the same age can have less in common than animals of a certain weight class (McNamara and Houston 1996). One characteristic element of phocid seals is the strong seasonal flux in energy intake and consumption associated with lactation, mating, moult and feeding (e.g., Ryg and Øritsland 1991). They all store energy mainly in form of blubber, and a schematic representation of the annual flux of the blubber layer is illustrated for the harbour seal in fig. 2. The birth of the single pups is followed by a short, intensive lactation period when females lose 30 to 50% of their total body weight, i.e., most of their energy reserves are consumed (Kovacs and Lavigne 1986, McCann et al. 1989, Hammill et al 1991, Haller et al 1996). An example of this is that grey seal females spend on average 85% of their energy reserves during lactation (Fedak and Anderson 1987). In harbour seal females the associated mean weight loss is about 40 % (Table 2) (Härkönen and Heide-Jørgensen 1990).

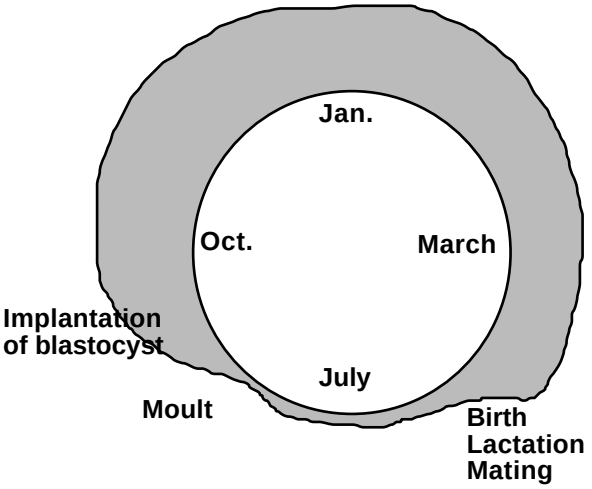

Fig. 2. *Schematic figure of the energy flux during the life cycle of an adult harbour seal in the Kattegatt-Skagerrak. The grey circle illustrates the strong flux in blubber thickness that is connected to the indicated major 'life cycle events'. The figure would be similar if drawn for any true seal (Phocidae), if the months are rotated to fit the cycle for each population. The figure is not in scale. The true size of the weight loss is exemplified in Table 1.*

Most phocid seals mate during or shortly after the lactation period (King 1983, Tinker et al. 1995). The mating systems vary, but in common is, that adult males consume a very high proportion of their energy reserves in the struggle for mating opportunities (Härkönen and Heide-Jørgensen 1990, Tinker et al. 1995). Consequently, both adult females and males are extremely lean after the breeding season. The next few months are spent feeding and the fat layers are re-built. The implantation of the blastocyst occurs about 4 months after mating (King 1983). Thus, the active gestation period is about 8 months. Another energetic constraint is imposed by the annual moult, when seals have to spend much time on land or ice in order to facilitate the vascularisation of hair follicles (Harrison and King 1973). In many species the optimal moulting time can probably over-lap with the time of restoration of fat reserves (King 1983, Thompson et al. 1989).

Table 1. *Mean weights of adult female harbour seals (Härkönen and Heide-Jørgensen 1990).*

Season	Post partum weight ± SE
May	72.4 ± 3.5 kg
June	58.0 ± 4.2 kg
July	48.9 ± 2.0 kg
August	45.9 ± 2.9 kg
Mean weight loss 37 %	

Phocid seals seem to be especially well adapted to regions with a strong seasonal, predictable flux in food availability and they are the most abundant mammals in the polar regions (Reijnders et al. 1993). Among the four species dealt with in this thesis the circum-polar Arctic ringed seal has the most northerly distribution. They are able to keep systems of breathing holes open in the thick fast ice, where they can be isolated from open sea for up to 8 months (Smith 1987). Their pups are normally born in lairs dug out in the snow. The crabeater seals do not keep breathing holes in the fast ice but spend their lives in the drifting sea ice around the Antarctic continent. Grey seals only occur in the northern Atlantic Ocean, where they are genetically differentiated into western and eastern Atlantic stocks (Boskovic et al. 1996). The majority of grey seal populations breed on land, whereas the Baltic and Canadian grey seal populations can switch between land- and ice breeding. The harbour seal (five sub-species) is abundant along most coastlines of the Northern hemisphere, both in the Atlantic and Pacific oceans. Harbour seals give birth on land (or in shallow water) and their pups are born without the lanugo, the white pup fur of phocid seals. The loss of the lanugo (which provides insulation in air, but only to a lesser extent in water) makes the harbour seal pups capable of entering the water immediately after their birth, but probably less well adapted to cold conditions of more northerly latitudes.

The character values of age specific haul out behaviour, mortality, fecundity and age of maturation vary both among species and between populations of the same species (Härkönen and Heide-Jörgensen 1990, Reijnders et al. 1993). These life history features can also vary for the same population among years. The remaining part of this thesis will investigate the origin and amplitude of such variations and their effects on the population dynamics of seals.

Environmental factors influence life history parameters

Food availability

Already the first glance on the global distribution of seals gives a hint on the importance of food availability. Regions with high primary production — upwelling regions, such as the eastern Pacific Ocean and the Antarctic Ocean — are the homes of hundred thousands of fur seals and millions of crabeater seals (Reijnders et al. 1993). In contrast, the nutrient poor areas such as the Mediterranean Sea and equatorial seas are sparsely inhabited by small and often dwindling seal populations (Reijnders et al. 1993). Also at the regional scale a positive correlation can be seen between the distribution of seal colonies and the sizes of the surrounding hunting grounds (Härkönen 1987a, Thompson et al 1996). At an even finer scale seal distribution has been correlated to the occurrence of dense fish shoals (Thompson et al 1991). Food availability can affect population growth via one or several of the vital life history features; reproduction, mortality or migration; Low food supply slows down body growth in seals (Fowler 1990, Kjellqwist et al. 1995), which in turn can delay the age at sexual maturity (Laws 1956). Inter-annual variations in food availability give different cohorts of the same population different rates of body growth prior to sexual maturity (Kjellqwist et al. 1995, Kingsley and Byers 1998). Therefore, it is not surprising that fluxes in the mean age at sexual maturity have been reported frequently in seals (Innes et al. 1981, Bengtson and Siniff 1981, Smith 1987, Kjellqwist *et al.* 1995, York 1983, Kingsley and Byers 1998).

Another food-mediated mechanism is that lowered fat reserves affect the reproductive rate of adult females (Smith 1987). Females in poor nutritive conditions (and/or with small body sizes) not only have lower pregnancy rates (Kingsley and Bryers 1998), but also smaller chances to complete the costly lactation (LeBoeuf et al. 1989). Small females produce smaller pups (LeBoeuf et al. 1989, Bowen et al. 1994), and since small body size of pups at weaning have been shown to lower juvenile survival rates (Bonner 1972), food availability will have a strong influence on the reproductive capacity of individuals. Adult mortality may also increase when food supplies decrease (Haug et al 1991). Lean adult females suffer higher mortality compared to fat sisters (LeBoeuf and Reiter 1988, Arnbom et al. 1994). Dramatic examples of food limited population growth rates are the mass starvation of harp seals in 1986-1988 (Kjellqwist et al. 1995), and the famous El Niño-effect which led to the death of thousands of Galapagos sea lions *(Zalophus californianus wollebaeki)* and fur seals *(Arctocephalus galapagoensis)* in 1982-1983 (Trillmich et al. 1986). Another example is the Arctic ringed seal, where close to complete reproductive failure occurred in the early 1970s in the western Canadian Arctic (Smith 1987). A similar event occurred 1984-1987 in the Amundsen Gulf (Canada), where the

reproductive failure was demonstrated to be associated with poor body conditions of adult females (Kingsley and Bryers 1998). Variations in food supplies can also dramatically change migration patterns as shown in harp seals (Haug et al. 1991).

Infectious diseases and parasites

Other potentially important external factors which affect the population dynamics of seals are infectious diseases and parasites. Many parasites such as hookworms (Acanthocephala), nematodes, lungworms (*Parafilaroides sp., Otostrongylus sp.),* and protozoans increase the mortality of seals in poor condition, e.g. due to mal-nutrition or to secondary infections (Haebler and Moeller 1993). Parasites can also increase the mortality in a more direct manner. Lung- and heart-worm *(Dipetalonema sp.)* parasites in the Wadden Sea mainly cause mortality among juvenile harbour seals (Breuer et al. 1988), and hookworm infestations in Baltic grey seals cause lethal colonic lesions (Bergman 1999). Bacterial infections are known to cause extra mortality in most species of seals (Anderson et al 1974, Baker 1987, Bergman 1999). Bacterial infections can also lead to high juvenile mortality in e.g. breeding colonies of grey seals (Baker 1980). Sudden mass deaths of marine mammals have been reported on several occasions (Heide-Jørgensen et al. 1992a). In the Antarctic a total mortality rate at 85% was observed among a group of 3 000 crabeater seals in 1955 (Laws and Taylor 1957). This mass mortality was possibly caused by canine distemper virus, CDV, introduced to the Antarctica by sledge dogs (Bengtson et al. 1991). Hundreds of American harbour seals *(Phoca vitulina concolor)* died as a result of an influenza A virus epizootic in 1979-1980 (Geraci et al. 1982). The Baikal seal *(Phoca sibirica)* had a canine distemper virus (CDV) outbreak in 1987 (Osterhaus et al. 1989). Most recently, the phocine distemper virus (PDV) epizootic (Osterhaus and Wedder 1988, Bergman et al. 1990) wiped out 55-60% of the continental European harbour seal stock during the summer of 1988 (Dietz et al. 1989, Heide-Jørgensen et al. 1992a).

Weather

Weather affects seal populations indirectly by the influence on the global climate which in turn affects the productivity of the oceans, and thus the abundance and productivity of prey species of seals. Temporal changes in large-scale weather systems such as the El Niño can have devastating effects by reducing food resources of seals (Trillmich et al. 1986). Long term climate changes also affect the distribution of seal species as illustrated by the Baltic ringed seal and the Saimaa seal *(Phoca*

hispida saimensis) which are relict species from the end of the last glaciation some 10 000 years ago.

Annual variations in weather conditions also influence seals as is the case of the Baltic Sea where grey seal females switch between land-breeding in warm winters to ice-breeding in cold winters. The mean weight of grey seal pups born on ice is about 20% higher compared with pups of land-breeding females (Jüssi 1999). The reason for this difference was hypothesised to be a consequence of a larger level of stress caused by crowding on the spatially limited rookeries (Jüssi 1999). Thus, access to ice as a breeding substrate possibly improves the reproductive success in grey seals (Jüssi 1999). Despite occasional reports of single ringed seal pups on land, Baltic ringed seals do not switch to land breeding at a large scale during warm winters, and their breeding success relies almost completely on the access to compact drift ice or thick fast ice. During mild winters large numbers of ringed seal pups are drowned and washed ashore (Härkönen et al. 1998). Another factor that affects the breeding success of ringed seals is snow depth. For excavation of breeding lairs snow depth should be about 45-130 cm (Lydersen and Gjertz 1986). In areas with limited snow coverage mortality rates of pups are usually considerably enhanced due to predation.

Predators and hunting

Predation as a regulating factor has been scarcely studied in seals, but has been postulated to be a crucial factor for seal abundance in some regions (McLaren and Smith 1985). Recovery of one fur seal colony in the Antarctic has been documented to be strongly reduced due to predation by leopard seals (*Hydrurga leptonix)* (Boveng et al 1998). Leopard seals are also known to prey heavily on crabeater seals, and up to 78% of adult seals have old scars from unsuccessful attacks (Siniff and Bengtsson 1977). Polar bears *Ursus maritimus* and arctic foxes *Alopex lagopus* are specialists on ringed seal pups (Lydersen and Gjertz 1986, Stirling and Øritsland 1995), but also wolves *Canis lupus*, red foxes *Vulpes vulpes* and wolverines *Gulo gulo* are known to prey upon ringed seals in the Arctic (Reeves 1998). Many populations, such as the Baltic grey seal, the Baltic ringed seal and the European harbour seal seem to be almost free from natural predators, although occasional seals may taken by killer whales (*Orcinus orca)* and white tailed eagles (*Haliaetus albicilla).*

Human hunt has repeatedly exterminated local seal populations and also decreased global population size to near extinction of several species. Examples of local extinctions are the large grey seal colonies in southern Baltic, the Kattegat, the Wadden Sea and Brittany (France) (Joensen et al. 1976, Pieur and Dugy 1978). One example of near global extinction is the Northern elephant seal, which was

intensively harvested during the 19th century until about 8 - 20 individuals were observed in surveys carried out in 1884 and 1892 (Cooper and Stewart 1983). After protective measures were taken the population increased exponetially and was estimated to about 125 000 in 1992 (Cooper and Stewart 1983). Another case is the Mediterranean Monk seal *Monachus monachus* which was deliberately killed by fishermen since it was regarded as a competitor. The global population of about 500 animals is still declining due to by-catches in fishing gear and the destruction of breeding habitats (Reijnders et al. 1993). A related species, the Caribbean monk seal *M. tropicalis* was severely overexploited and is now regarded extinct (LeBoeuf et al. 1986). The small population of some 200 animals of the Saimaa ringed seal is a result of over-exploitation combined with interactions with the fishery, and the destruction of the breeding habitat (Ranta et al. 1996, Kokko et al. 1997; 1998). The effect of the hunt does not only depend on the numbers of killed animals, but also on the age structure of catches (Kokko et al. 1999, II). This will be discussed below in more detail.

Toxins

The influence from environmental toxins on population growth is either instantly exhibited as increased mortality or indirectly via diverse disease complexes (Bergman and Olsson 1986, Reijnders et al. 1993). Polychlorinated biphenyls (PCBs) and many other organochlorines (OCs) accumulate in the food chains, and top predators such as raptorial and piscivorious birds as well as seals can to carry very high concentrations in their body tissues (Olsson 1977, Olsson and Reutergardh 1986).

In populations of harbour seals, concentrations of PCBs vary with the level of industrialisation and the extent of water exchange of different sea regions. This is demonstrated by mean values of concentrations of different PCB fractions in harbour seals in the Atlantic, where Icelandic harbour seals have the lowest concentrations of about 1.5-5.0 parts per million (PPM) lipid, while the heavily industrialised and enclosed St Lawrence Estuary show concentrations about 17.1 PPM. The harbour seals in the Baltic Sea and Wadden Sea have mean concentrations of 85 PPM lipid (Bernt et al. 1999). The effects of high levels of PCBs are generally very difficult to quantify. One reason is that levels of PCBs vary substantially depending on which part of the season, which age groups, individuals and which parts of the body are sampled (Safe 1984, Bignert et al. 1993). However, a controlled feeding experiment revealed lowered pregnancy rates in seals fed with Baltic herring compared to the control group that got North Sea herring (Reijnders 1986). In another experiment two groups of 11 harbour seals pups were fed with Baltic herring and North sea herring, respectively, during a time span of 2,5 years (de Swart 1995). Despite the fact that

the seals fed with Baltic herring only reached a mean PCB concentration of 16.5 PPM, a statistically significant 25% decline in the level of natural killer cells was detected in this group compared to the 'North Sea group' (De Swart 1995).

The Baltic ringed and grey seal populations have been exposed to an uncontrolled full scale experiment. The mean level of PCB in seals from the northern Baltic proper was about 450 PPM lipid in the early 1970s, which eventually has declined to considerably lower values in accordance with lower concentrations in their prey (Jensen et al. 1976, Olsson 1977, Bignert et al. 1998). A sample of 225 adult ringed seal females revealed an alarmingly low pregnancy rate of 30% which dropped further to 20% during the period 1973-1979 (Helle 1980b). The cause of the low reproductive rates was largely explained by occlusions in the uterine horns. The prevalence of this pathological change increased from 35% to 59% during the same time period (Helle 1980b). The occlusions caused permanent sterility in ringed seals and the frequency of occlusions also increased with the age of the animals (Helle 1979; 1980a; 1980b). Also in grey seals, severe reproductive disturbances were documented (Bergman and Olsson 1986, Bergman 1999). An underlying cause of some of the toxic effects of PCBs may be alterations in hormonal levels (Bäcklin 1996). Experiments carried out on mink *Mustela vison* showed that the early formation of the placenta is disrupted in animals exposed to PCBs, which leads to the death of the foetus (Bäcklin 1996).

Conclusions on life history features

.The basic life history features set the upper limit for the reproductive capacity of individuals. (E.g. Seals seldom give birth to pups before 4 years of age, and no seal females have been seen to successfully rear more than one pup per breeding season and very few individuals reach ages exceeding 40 years.) These limitations are basically similar for all pinnipeds and are probably partly caused by phylogenetic constraints. However, there is a considerable variation downwards, *e.g.* the age at first parturition can occur as late as at ten years of age (Kingsley and Byers 1998), birth intervals can exceed one year, and pup mortality can be very high (Smith 1987). Thus, the upper theoretical reproductive capacity is seldom realised. At the individual level this can be understood in terms of energetic constraints which introduce trade-offs among life history features. Thus, energy allocated to reproduction a given year can reduce future survival and/or future reproduction. Trade-offs produce situations where animals can be said to 'adopt different strategies' (e.g. to reproduce quickly and die young, or to get a heavy pup with high survival every second year, instead of getting a tiny pup each year). Such strategies can be evaluated in terms of maximisation of long-term inter-generation fitness (Houston and McNamara 1999). The importance and impact of life-history trade-offs can be expected to vary

considerably, since energetic constraints typically vary among species of seals, different populations of the same species as well as among years.

The upper limit of individual reproductive rate is reflected at the population level and gives an upper theoretical limit for the population rate of increase. The mean values of fecundity and mortality will always be lower than the theoretical maximum rate of increase, also for populations which live under favourable conditions. Chance events such as failed fertilisation or early abortions reduce annual pregnancy rates. Mean pregnancy rates rarely reach 0. 96 in samples of reasonable sizes (Boulva and McLaren 1979, Bigg 1969, Härkönen and Heide-Jørgensen 1990). Another factor that will decrease mean pregnancy rates is senescence (Härkönen and Heide-Jorgensen 1990). Further, environmental factors such as those described in the preceding paragraphs will reduce fecundity and survival. The impact from external factors may occur with different frequency and amplitude. Environmental pollution and high burdens of parasites can decrease population-specific long term averages of fecundity and survival, while epizootic outbreaks and excessive hunting have the capacity to drastically reduce population numbers on a more short-term basis. The type of variation in fecundity and survival rates will determine the structure of each population. Seal populations are structured into age and sex classes which in turn are distributed in time and space. In a population with a constant rate of increase (thus no temporal variability among years), the age- and sex-structure quickly reaches a stable distribution, where the frequencies of individuals at each age class are constant (Lotka 1956). Populations with low juvenile survival typically have steeper age distributions compared to populations with higher juvenile survival rates (Caswell 1989). Short term changes in the basic life history parameters will temporally perturb the population composition from the stable structure. Long-term changes in fecundity and survival will lead to a new, different stable age structure. The population composition will determine the population growth rate and the population size (Fig. 1). The aim of this thesis is to better understand these mechanisms, that govern the dynamics of seal populations.

About chapters I-V

The following chapters will present different types of time-series data on the dynamics of four species of seals; the crabeater seal (I), grey seal and ringed seal (II) and the harbour seal (III, IV, V). The interpretation of these data depends crucially on methods for sampling and data analysis. Therefore, several methodological issues will be addressed: Two different ways to assess the mean age of sexual maturity are evaluated (I). A method to estimate historical population size is developed to account for the structure by age and sex of the catches (II). A new branding technique that allows recognition of individual seals through-out their lives is described (III). The

detailed data on age and sex specific behaviour, which is obtained by the new method, can be used to improve estimates of fecundity, mortality and long term population growth (III). Estimates of spatial segregation by sex and age can be used to determine the relevant spatial scale at which various population processes should be studied (IV). Finally, the importance of initial age- and sex-structure for evaluations of trend analyses is highlighted, and a ready-reckoner by which unlikely growth rates can be detected is presented (V).

In the following paragraphs the basic conclusions on each method are summarised. Thereafter–some aspects of the new information on the population biology of the included species are discussed in relation to earlier work.

Crabeater seals and the age at sexual maturation (I).

Mean age at sexual maturity in seals is mostly assessed by counting numbers of ovarian corpora in the ovaries of animals of known age. Age is estimated by counting numbers of growth layer groups in teeth (Dietz et al. 1991). Two main approaches have been used to determine the age at maturity, one direct, one indirect. The first method uses the presence of a corpus luteum at the year of collection, which indicates that an ovulation has occurred. The proportion of females that have ovulated is then calculated for each age class (DeMaster 1978, York 1983). The indirect method relies on ovarian 'scars' from past ovulations, corpora albicantia, (Bengtson and Siniff 1981, Boyd 1984). By substracting the number of corpora albicantia from the age of the seal, the age at first ovulation can be estimated. Both methods were applied to three samples from crabeater seals collected in 1964, 1977 and 1989, respectively (I). The two methods produced similar estimates of age at sexual maturity for the 1964 and 1977 samples, whereas the results for the 1989 sample differed significantly between methods. The in-built biases of the two methods and the differences between the sampling events were scrutinised (I). It was found that the direct method is sensitive to biases in the age structure of samples, whereas the indirect method is not. The indirect method relies on assumptions on a single annual ovulation, and that all small corpora are registered. The indirect method is likely to be less useful in species with high resorption rates of corpora albicantia, such as grey seals (Boyd 1984) and harbour seals (Härkönen and Heide-Jørgensen 1990). The classification of individual maturity status is more rigid in the direct method, and can thus be used to correctly assess the age at sexual maturity if samples are representative of the population. The indirect method can be useful as an index of age at sexual maturity, also in skewed samples, if the rules of classification are standardised (I).

The estimated age at sexual maturity of 6.57 ± 0.82 is considerably higher than described earlier for the species (I). It will have implications for the modelling of population age structure which until now have used ages at first birth at about 4 years (Boveng 1993). Both methods indicated a significant increase in age at sexual maturity in the 1989 sample compared to earlier years. The indication of a true increase in age at sexual maturity in 1989 is in concordance with earlier studies on age at sexual maturity that have described an increasing trend since the 1960s (Bengtson and Laws 1985). What are then the reasons for the variations in age at sexual maturity in crabeater seals? The heavy exploitation of the large baleen whale stocks were hypothesised to increase the food availability for krill eating animals (e.g. Laws 1977b). The increased food availability would have lead to increased rate of body growth in crabeater seals and thus decreased age at sexual maturity (Laws 1977a, Bengtsson and Laws 1985). Similarly, the subsequent recovery of the baleen whales has been suggested to be the cause behind a detected increase in the age at sexual maturity of crabeaters (Bengtsson and Laws 1985). However, the task to convincingly link such ecosystem processes is difficult. A fundamental pitfall in this case is to estimate historical changes in krill abundance. The difficulty of getting statistically reliable estimates of the abundance of krill even nowadays is due to the very patchy distribution of krill. “It is even possible for the majority of krill biomass in a study area to be found in one very dense swarm that is likely to be smaller in extent than the typical distance between survey transects (i.e. easily missed)” (Boveng 1996; p 88). An additional complication arises since up to half of the water masses can be replaced within the course of one survey replication (Boveng 1996). Further, the crabeater seal is one of the most abundant large mammals in the world, but good estimates of population size is very difficult to obtain due to their wide distribution in the drifting pack ice. They mostly haul out in ‘family groups’ of three, but occasional clumps of up to 600 individuals per square kilometre makes extrapolations from aerial surveys uncertain. However, estimates of about 11 millions are given (Gilbert and Erickson 1977, Erickson and Hanson 1990).

There are other evidences for major fluctuations in the crabeater seal population. Age structure samples of crabeater seals typically show 4-5 year fluctuations in cohort strengths. These fluctuations have been suggested to be cyclic (Laws 1984, Bengtson and Laws 1985, Testa et al. 1991). Careful statistical analysis revealed that although the fluctuations are true demographic fluxes (and not due to artefactual sampling etc.), they are not periodic. Neither could the fluctuations be correlated to extent of sea ice, surface air temperature, a measure of the Southern Oscillation, nor the number of leopard seals (Boveng 1993). It seems likely that the change in age at sexual maturity described in chapter I, can be related to the recurring fluxes in cohort strength. However, this hypothesis remains to be critically tested. A correlation between age at sexual maturity and cohort strength would suggest that the cause of both phenomena could be related to food availability, since decreased food availability can lead to both decreased age at sexual maturity and significantly reduced fertility rates of adult females (e.g. Kjellqvist et al. 1995)

Baltic ringed and grey seals and their historical population sizes (II)

Data on hunting mortality can be used to retrospectively estimate the historical population sizes of populations (Smith 1983). The data needed are; as good estimates as possible on the annual hunting mortality and of the vital parameters of the population. A variant of Lotka's growth equation (Lotka 1956) was then used to back-calculate the numbers of seals that must have been alive in the previous year to be able to sustain the size of the recorded hunting mortality (Smith 1983). This model presumes a stable age and sex structure of catches. However, hunting directed towards adult females is much more costly for the population compared with hunting focused on pups. Therefore, the model was developed to also take age and sex composition of catches into account (II). Sweden and Finland initiated a 70 year long 'war against the terrible fish eaters' (Lönnberg 1898) in the beginning of the 20th century. From the year 1900 and until 1940, 380 990 bounties for ringed seals were paid. After 1940 the annual catches dropped steadily despite access to better weapons and increased hunting effort (II).

The Nordic bureaucracies have produced one of the best records in the world on how seal populations are hunted down to very low numbers. The documentation included not only numbers of killed seals, but also species, gross age structure (juvenile/older), hunting method and hunting area. This gave an unique opportunity to retrospectively estimate the historical population sizes of the two seal species during a time span of one hundred years. The estimate obtained by this method is a minimum value. We found that the recorded hunt was possible only if the initial population sizes were at least 88 000-100 000 grey seals and 190 000 -220 000 ringed seals. Lower numbers of seals would require impossible combinations of vital parameters. The aim to find the lowest possible population sizes guided us in choices that would otherwise have been difficult. The age structure of the historical population and the intrinsic rate of increase are unknown parameters. However, since assumed high rates of increase lead to lower historical populations the maximum rates of increase that is known for the species was chosen (II). Similarly, the initial age structures which produced the lowest estimate of historical abundance were chosen (II). An estimate of the upper border on how many seals there might have been in the Baltic was not attempted. Assuming significantly lower fertility, or un-recorded mortality (say due to years with little ice for reproduction, or an unknown disease) can easily produce very high estimates of historical population sizes (even up to one million or more).

A different approach to estimate historical population sizes for these two populations has been applied. Instead of counting backwards, the probability that a given initial population sizes in the beginning of the 20^{th} century will lead to the present population sizes can be assessed (Kokko et al 1999). Many different initial population sizes were simulated within a wide range of hypothetical life history parameters and assumed age distributions of the catches. Their study confirms that

assumed high growth rates make lower initial population sizes possible. Further, it shows that increasing the variance in population growth rates presumes larger initial population sizes ('a few bad years cost more than a few good years'). The initial sizes of the populations obtained by this method suggest that numbers of ringed seals with 95% probability were between 50 000 and 450 000 and grey seal numbers between 30 000 and 200 000 (Kokko et al. 1999). The lower ranges of these intervals are unrealistically low, since they are based on a long-term growth rate of λ=1.15, which is impossible for these species (V). Also, the lower ranges are the result of scenarios where only juveniles were assumed to be killed. The ringed seal hunt was directed towards adults, and the grey seal hunt included both pups and breeding females (II). Lack of detailed data on size and age structure of hunting mortality can be compensated by simulating many hypothetical scenarios, however it also leads to wide confidence limits of estimated initial population size (Kokko et al. 1999).

Our method to estimate former population sizes based on hunting statistics is most powerful during periods with high hunting mortality (II), since it tells 'how many seals there must have been at least to sustain the recorded hunt'. Consequently, the sharp decline in both populations from 1900 to 1940 are well described, while the population sizes during the 1950s and early 1960s could have been larger and then declined even more dramatically during the 1970s (Figs 9 and 10 in chapter II). Sterility linked to organochlorine pollution is probably the main explanation for the slow recovery after hunting was banned in 1988. During the 1970s burdens of OCs decreased in the Baltic (Bignert et al. 1993) and the population rate of increase started to rise slowly during the 1980s. Annual rates of increase in grey and ringed seals during the 1990s were estimated to 6.5% and 5%, respectively (Härkönen et al. 1998, Helander 2000). Ground and aerial surveys carried out in 1998 revealed that the size of the grey seal population was approximately 7600 (Helander and Härkönen 1999) while numbers of hauled-out ringed seals in 1996 amounted to 5500 animals (Härkönen et al. 1998). The Baltic ringed and grey seals are still far from their historical abundances, and should according to deterministic views be able to increase exponentially. However, several factors slow down the recovery. In addition to remaining reproductive disturbances (Mattson and Helle 1995) also new health problems, including immuno suppression, are reported in grey seals (Bergman 1999). Especially grey seals, but also ringed seals are by-caught in considerable numbers in fishing gear. The ringed seals in the Gulf of Finland suffered severe losses in 1991 due to a mass mortality, when perhaps half of the stock died for unknown reasons (Stenman and Westerling 1995). Only some 250 animals remain in the area at present (Härkönen et al. 1998). Thus, despite generally increasing populations considerable care should be taken to establish population sizes and rates of increase in order to assess the future of these seal populations.

Harbour seals (III-V)

Quantifying temporal distribution (III)

Freeze-branding provides a new opportunity to study long term behaviour of seals (III). The benefit of this method is that it gives individual permanent brands, that are visible at distances up to 500 meters. Techniques with equipment glued to the fur, such as radio-tagging (Thompson 1989, Yochem et al. 1987), and satellite tags (Heide Jorgensen et al. 1992c) can provide much more fine-scaled data but are limited to less than one year because of the annual moult. Many attempts have been made to develop permanent methods of branding. The most wide spread is to attach roto-tags to the hind flippers (Summers and Mountford 1975, Wiig and Øien 1988). The problems with roto-tags are that they are too small to read at distance, and thus re-sightings are few and mostly from dead animals (Øien and Øritsland 1995). Another problem is that roto-tags can get entangled in fishing nets and lead to wounds or even the death of its bearer. Re-sighting data from freeze-branded animals, adjusted for the number of alive branded animals in each year and the observation effort, give robust estimates of temporal and spatial distribution of seals by sex and age (III, IV).

The study of the temporal distribution of 163 harbour seals revealed a conspicuous seasonal age and sex related haul out behaviour (III). This segregational behaviour of population segments lead to permanently skewed population compositions on land during the entire study period (30 May-12 September). The observation of skewed compositions of haul out groups underlines earlier warnings against the common assumption that samples of seals are representative of the entire population (Thompson 1989, Thompson et al. 1989). Further, when the true underlying age structure is skewed, the different haul out behaviours of population segments will lead to artefactual variations in estimated growth rates e.g. the total haul-out tendency of a population with mostly young seals will differ from a population with a high proportion of adult males. This feature was shown to produce artefactual variations in estimated population sizes of harbour seals ranging between –16 to 6% (III). The observed different temporal distribution by sex and age in harbour seals on land is most probably related to the life history events, such as breeding, lactation and moult (Thompson et al.1989). Thus, segregational behaviour can be expected to be found in most other seal species. However, if sex and age related seasonal behaviour can be quantified population estimates can be compensated retrospectively (III).

Quantifying spatial distribution (IV)

Data on resightings of freeze-branded harbour seals were analysed with regard to spatial distribution of seals by sex and age. The main finding was a striking site fidelity in adult females, as they mainly stay at the site where they were branded as pups. The site fidelity in females two years and older increased with increasing age. Juvenile females and all age classes of males utilised the surrounding haul-out sites extensively, especially during the moulting season. However no resightings were made outside a 32 km range from the branding site (IV). The age and sex specific pattern of distribution of the branded animals was assumed to reflect seasonal migrations of the harbour seal population. This is in concordance with results from radio-tagged harbour seals where migrations among nearby colonies were documented at the individual level (Thompson 1989, Thompson et al. 1996). Independent data on the spread of the seal epizootic and the distribution of the pup production among seal localities in the Skagerrak support the found migration patterns from the branded seals. Discrepancies in the scale of sampling regimes and the actual population structure can lead to artefactual estimates of population growth trends and to over-estimated rates of gene flow (IV). Similarly, feeding studies performed at few localities may not reflect the feeding habits of the population, but could be biased towards, e.g., young males or adult females. Except for sampling biases the strong spatial segregation of harbour seals is likely to profoundly affect the gene flow and the spread of diseases and parasites (IV). This will be discussed more thoroughly below.

The influence of initial conditions on population growth (V)

The post-epizootic development of the populations in the Kattegat and the Skagerrak was documented by annual aerial surveys during the period 1988 to 1998 (V). An unusually high rate of increase (λ =1.16) was observed in the northern region (The Skagerrak) whereas the growth rate was significantly lower (λ=1.10) in the southern region (the Kattegatt). The skewed mortality during the epizootic led to a biased age structure of the whole surviving population (Heide-Jørgenssen et al. 1992b) which also differed between regions (V). Harbour seals show strong site fidelity (IV), which is why regional differences in age-specific mortality at the year of the epizootic were expected to have persisted and influenced the subsequent population growth rate. In the Skagerrak relatively more males than females died, while the mortality in the Kattegatt was slightly female-biased. The high population growth rate in the Skagerrak could be explained by simulating the age- and sex-structure of the survivors (V).

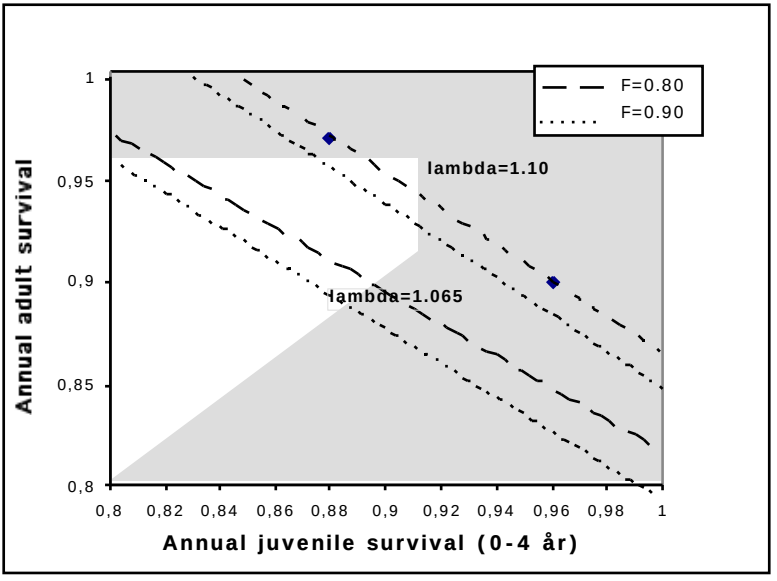

Fig. 4. *A ready-reckoner for grey seals. The shaded area indicates unlikely combinations of long term vital parameters in a stable population. Subadult survival is never found to exceed adult survival, adult survival above 0.96 and subadult survival above 0.93 is also very rare. The mean age at first parturition is set to 5 years. The combinations of juvenile and adult survival which lead to population growth rates of 1.10 and 1.065 are indicated. The fertility rate also affects the possible combinations.*

However, the growth rate in the Kattegat remained low also after the effect of initial age structure had been removed (V). It is interesting to note that also the harbour seal population in the Wadden Sea showed a remarkably high annual growth rate after the epizootic (Reijnders et al. 1997), which coincides with the situation in the Skagerrak. The Wadden Sea was hit by the disease during peak moult when males are strongly over-represented on land (III, Thompson 1989), which could have led to a female-biased composition of survivors also in the Wadden Sea. The high rate of increase supports a possible correlation between seal behaviour and mortality patterns during the epizootic (above). The low growth rate in the Kattegat region is a true indication on that the long-term capacity of increase is lower compared with the Skagerrak. Factors which might be connected to the lowered growth rate are feeding habits (Härkönen 1987a), availability of haul-out sites (Härkönen 1987b) and the frequency of bone lesions (Mortensen et al. 1992), which all are known to differ between the regions. The future will tell if any of these factors are involved.

A ready-reckoner was developed by which unlikely growth rates can be detected. The upper limits of fecundity and survival rates of any population give the upper limit for the population growth rate, when age and sex composition is stable. The ready-reckoner can also be used the other way round i.e. to find the possible ranges of parameter values that can explain a found growth rate. Seal populations can not have long-term growth rates exceeding $\lambda = 1.13$ (V). For species such as grey seals and ringed seals the maximum growth rate is about 1.10, because of older age at first parturition and lower mean life-time pregnancy rates (Fig. 4). Frequently reported higher estimates in the literature are indicative of sampling biases or unstable population compositions (V).

The harbour seals

Background

The Kattegatt-Skagerrak harbour seal population has varied in size over the last hundred years. In the early 20th century it numbed to about 18000 (Heide-Jørgensen & Härkönen 1988). Intensive hunting resulted in a drop to about 1500 seals up to the late 1960s, when hunting was banned and protective measures were taken (Heide-Jørgensen and Härkönen 1988). After 1978 the population increased exponentially at 11% per year until 1987 when the population size was estimated to about 9000 (Heide-Jørgensen et al 1992b). In 1988 an epizootic disease reduced the population to about 3500 animals. In the autumn of year 2000 the seal stock exceeded pre-epizootic size and was estimated to about 16000 (Härkönen unpubl.). The age and sex specific behaviour provide new insights both on the mortality patterns during the epizootic and the subsequent rate of recovery (III-V).

The 1988 epizootic revisited

The mass death of harbour seals in 1988 was caused by an outbreak of a previously un-described morbilli virus, (Phocine Distemper Virus (PDV) (Osterhaus and Vedder 1988)). The mortality rate differed among regions, where the highest moralities were detected in the Kattegatt, the Skagerrak and the Wadden Sea, whereas the British and Scottish colonies suffered lower losses (Dietz et al. 1989, Heide-Jørgensen et al. 1992a, Thompson et al. 1992). The mortality pattern was suggested to be linked to environmental pollution since mortality rates were larger in regions with high burdens of immuno suppressive OC's (de Swart 1995). Although plausible, it has proved difficult to establish a link between OC's and the severity of the PDV outbreak. Accordingly, a comparative study on PCB levels of the victims and survivors of the epizootic in England did not lead to any conclusive evidence (Hall et

al. 1992). One major obstacle in such comparisons is the extreme variation in concentrations of OC's among samples.

An alternative explanation for the large mortality in European harbour seals was proposed by Kappe et al. (1997): 'There is a striking correlation between low levels of genetic variation and susceptibility to the Phocine Distemper Virus (PDV)'. However, there are no studies supporting a link between low genetic variation and susceptibility to PDV. Further, the genetic variability of European harbour seals has not been found to be unusually low in other genetic screenings (Stanley et al. 1996, Goodman 1998). A third proposed explanation for the high mortality was simply that the European harbour seals had not earlier been exposed to this highly lethal virus (Have et al. 1991, Heide-Jørgensen et al. 1992b). Several similar incidents of virus-induced mass deaths have occurred prior to the introduction of organochlorines in unexploited stocks of marine mammals e.g. in the Antarctic crabeater seal in the 1950s (Laws and Taylor 1957).

The seasonal age- and sex-dependent haul-out behaviour (III, IV) add other possible clues to the mortality patterns during the epizootic. The harbour seal colonies were hit by the disease in sequence, i.e. the peaks of the epizootic curves for different localities showed a temporal cline from late May to late October (Dietz et al. 1989, Swinton et al. 1998). The new data on haul-out behaviour, which encompass the period from 30 May to 12 September, demonstrate conspicuous fluxes in the number and the composition of seals on land during the entire period (III). The age and sex structure of the victims of the epizootic can be compared with the expected distribution from a stable age structure (V). Results from annual surveys of the total population coupled with pup counts prior to the epizootic motivate the assumption of a stable age structure in 1987 (Heide-Jørgensen et al. 1992b, V). Almost all pups of the year died during the epizootic. The sub-adults (1-5 year-olds) survived the disease to a much higher extent compared with adults: The segment of 1-5 year-olds comprise 60% of all animals (one year and older) in a harbour seal population with a stable age structure (V), but among the victims of the epizootic this segment only amounted to 35% of all dead seals (one year and older) in the Kattegatt and 45% in the Skagerrak.

The sex ratio of the dead sub-adults did not deviate from 52% males as predicted by a stable age structure (the Skagerrak 49%, the Kattegatt 52%). However, the sex ratio of the dead adult seals (6 years and older) differed among localities. The colonies which were hit by the disease early in the season showed a lower proportion of males among the victims as compared to colonies which were infected late in the season (Fig. 3, III). Thus, the sex ratio of the victims of the epizootic is correlated to the sex ratio of seals on land at the time of infection in the Kattegat-Skagerack (Fig. 3). This indicates that some behavioural trait influenced the risk of individuals to get infected. It questions the common assumption of homogenous mixing within local populations in epidemiological modellings of the epizootic (Swinton et al. 1998, De Koeijer et al.

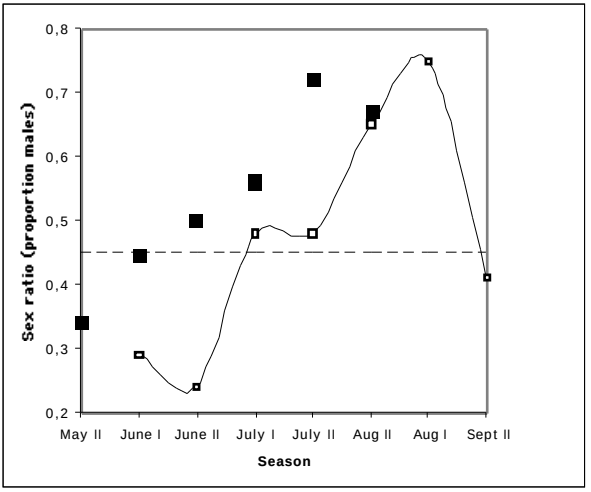

Fig. 3. *Seasonal flux in sex ratio among adult harbour seals on land (thin line), (data from paper III). Black squares are the sex ratio of the adult victims of the epizootic in 1988. From the left; Anholt (n=38, Hesselø n=45, Varberg n=22, Onsala n=58, Lysekil n=25, Koster n=227) Partly unpublished data. Dotted line indicates the 45% males that are expected in harbour seal populations with a stable age structure.*

1998). It is also apparent that the sub-adults were less sensitive to the disease, since they are well represented on land during the entire period (III). Further, males suffered higher mortality rates compared with females at all colonies (Fig. 3). This different sensitivity to the disease by age and sex is also neglected by unstructured epidemiological models.

The regional variations in mortality patterns between the Kattegatt and the Skagerrak were probably related to behavioural traits that also could be reflected in the haul-out behaviour. The PDV belong to the morbilli viruses which usually are transferred to neighbours by coughing (Koeijer et al. 1998). The level of exposure to the virus, depends on the rate of contacts between individual seals. It seems likely that the rate of contact varies over the season when the seals pass the major life history events: Lactation (May-June, when the disease struck the Kattegat), mating (July) when the Skagerrak was hit by the disease) and moulting (August). If so, it could be hypothesised that mortality patterns also in other regions of Europe were affected by the composition and behaviour of haul-out groups at the time of infection (Harwood et al. 1989). This idea cannot be appropriately tested since detailed data on the age structure of the victims are lacking for other regions. However, the total mortality and the peaks of infection are know for other regions (summarised by Swinton et al.

1998). Very high mortality rates were observed in the Wadden Sea where the peak of the epizootic occurred in late August, which coincides with peak moulting season (III, Thompson 1989). In northern Scotland, the total mortality was only about 10-20 % (Thompson et al. 1992). The peak infection time in Scottish populations occurred in September (Swinton et al. 1998), when seals spend less time on land (Thompson 1989, Thompson et al. 1989). In a sample of 68 Scottish seals, 52% were estimated to have been exposed to PDV. The frequency of infection is not known from other areas, but the rapid development of the disease in haulout groups of the Kattegat, the Skagerrak and the Wadden sea indicates that a much higher proportion of the seals encountered the virus in these regions (Heide-Jørgensen et al. 1992a, Koeijer et al. 1998).

Epidemiological modelling of the PDV epizootic showed that different assumed survival rates of infected individuals was the most important parameter for the over-all survival rates of the population, under the condition that the 'rate of spread of the disease' (R_0) is above 2.0 (Koeijer et al. 1998). Their interpretation of this result was that the higher observed survival rate among Scottish seals could be linked to better health. They estimated that R_0 values were above 2.0 in all regions. However, it is notoriously difficult to estimate R_0, especially without knowledge about behavioural differences among groups of seals:

$$R_0 = \alpha / \beta$$

where α = the average number of contacts of an infectious animal per unit time multiplied with the probability of spreading the infection during such a contact, and where β = 1/ infection time (Koeijer et al. 1998). Thus, mean α-values can be expected to change when the number, and composition of seals change over the season. This would imply that also R_0 will vary. If R_0 is allowed to decrease below 2.0 in the model of Koeijer et al. the expected mean survival of the population is suddenly affected substantially by the precise value of R_0 (Koeijer et al. 1998). (E.g. if the survival of infected individuals is fixed at 50% the corresponding total survival of the population is about 50% at $R_0 > 2.0$, but as high as 75% for $R_0 = 1.2$. (Fig.1. Koeijer et al. 1998).) Thus, the rate of contact between seals at different localities could theoretically lead to large differences in over-all mortality rates between regions, also if there were no regional differences in the survival of infected individuals. An age structured epidemiological model is needed to quantify the effects of this feature on the course of the PDV epizootic. In any case, synergistic effects from pollutants should not be ruled out. High prevalence of bone lesions among adult harbour seals in the Kattegat- Skagerrak indicates that hormonal imbalances in fact were present (Mortensen et al. 1992). However, in order to compare mortality rates among regions, the spatio-temporal distribution and behaviour of seals at the time of infection should be taken into account. Not before

such biases are removed, other explanations such as impaired immune systems or low heterozygoty can be evaluated accurately.

Population growth and regulation of seals

Many seal populations have been heavily exploited during the 19th and 20th centuries (see above and II). Local populations have been wiped out, but amazingly, only one species has become globally extinct (LeBoeuf et al. 1986). Growth in recovering seal populations is often well described for long time spans by deterministic exponential models (Cooper and Stewart 1983). Reliable projections of future development can be made during such periods (Heide-Jørgensen et al. 1992b) if the initial structure and life history parameters are known (V). However, the exponential increase never goes on for ever. Hence, some central questions are: Which factors govern the population dynamics of seals? How much are seal populations affected by chance events in birth and death rates (demographic stochasticity), recurrent environmental fluxes (environmental stochasticity) and sporadic catastrophes? Further, is density dependence important?

Demographic stochasticity is a threat when populations are small (Burgman et al. 1993). Since seal populations are structured by sex and age the required population size for being safe from extinction by demographic stochasticity is dependent on the population structure. A stable, panmictic seal population of 100 individuals and with a positive growth rate will equal a larger ‘demographic effective population’ (Kokko and Ebenhard 1996). Longevity constitutes a protection against demographic stochasticity, which might explain why many seal populations have managed to recover from extremely low numbers (Cooper and Stewart 1983, Reijnders et al. 1993).

It is a common view that seal populations are regulated by density dependence, where increasing numbers of seals imply a gradually reduced rate of increase, although this view has been questioned (McLaren and Smith 1985). One proposed functional mechanism is mediated via food competition, that would reduce fecundity and survival (Fowler 1990). Although food availability is a crucial factor in the dynamics of many seal populations, it is notoriously difficult to detect weather food shortage is due to the number of seals or, if it is a result of seal-independent reduction of the prey population. The mass starvation of harp seals in 1987-1988 indeed reduced fecundity and survival rates (Kjellqwist et al. 1995), but the lack of seal-food (capelin and polar cod) was probably caused by lowered production of fish-food (krill) and most unlikely related to the population size of harp seals. However, once the fish stocks crashed, seal population size can be expected to have accentuated the catastrophe by food competition among seals.

Another possible mechanism for density dependence in seals could be competition for breeding grounds (McLaren and Smith 1985). In ringed seals, dominant females are found in the best breeding ice, whereas younger females are reduced to less favourable areas with enhanced predation risk for their pups (Smith and Lydersen 1991). Another phenomenon that has been linked to density dependence is dispersal of diseases. Increased pup mortality due to bacterial infections in grey seal colonies are suggested to be correlated to herd size (Baker 1980, Stenman and Westerling 1995, Jüssi 1999). It seems likely that density dependent mechanisms do operate in seal populations, however their occurrence and impact can rely on random events, such as the sudden collapse of a food web or the details of the annual formation of sea ice.

The ecosystems in which different species of seals live are characterised by different levels of environmental stochasticity. The sensitivity to such variations can in part be related to the feeding ecology of the species. Some seals such as the European harbour seals are generalists, which prey upon more than 30 fish species (Härkönen 1987a,b, Härkönen and Heide-Jørgensen 1990, Tollit and Thompson 1996), which provides a possibility to switch prey when variations occur in the relative abundance of different fish stocks. Contrastingly, the Antarctic crabeater seal preys almost entirely on krill (Bengtson 1982). Obviously, it can be expected that seals that rely on a few variable prey species are more likely to suffer from environmental stochasticity. Perhaps the fluxes in cohort strength (Boveng 1993) and in age at sexual maturity (I) of the unexploited Antarctic crabeater seal population are indicative of a population limited by a variable food supply?

External density independent factors can have large impact on seal populations. Some occur as sudden ‘catastrophes’ as exemplified by the harbour seal epizootic in 1988 (Dietz et al. 1989). Other external influences, such as the lowered reproduction linked to PCB-pollution act slowly over long time periods and reduce the parameter values of fecundity and survival (Bergman 1999). The reason why the spread of the harbour seal epizootic in 1988 was density independent is due to the fact that harbour seals mostly haul out close together on land (Heide-Jørgensen and Härkönen 1992, Swinton et al. 1998). From the virus’ point of view a harbour seal colony of 200 individuals is as dense as a population of 2000 (Heide-Jørgensen and Härkönen 1992). (Under the assumption that they have the same composition by sex and age, and are infected during the same time of the year). This independence of host population size is likely to be true for the spread of virulent diseases in other ‘social’ seals, such as grey seals and elephant seals (Koeijer et al. 1998).

The occurrence of the epizootic draw attention to the phenomenon of mass deaths in marine mammals in general and reviews revealed that mass deaths were not such a rare event (Heide-Jørgensen et al 1992a, Harwood and Hall 1990). E.g. mass deaths of harbour seals were reported in the Orkneys in 1813, 1836, 1869-70 and in Shetland 1930 (Harwood and Hall 1990). The indications that diseases which cause

high mortality are recurrent events in seals led to the suggestion that the persistence of many seal populations is governed by outbreaks of diseases (Harwood and Hall 1990). Although the occurrence of mass mortalities are spectacular and potentially important for regulation of seal populations the historical accounts are anecdotal and the causes for the earlier diseases remain unknown. It is therefore difficult to evaluate the importance of disease in the population dynamics of seals. The apparent correlation between fluxes in food availability and rate of population increase remains a powerful explanation to the long term abundance of seals. The relative importance of environmental stochasticity contra catastrophes for each population will depend on the mean and the variance of the population growth rate and the magnitude and frequency of the catastrophes (Lande 1993).

Spatial subdivision of a population, into many weakly connected sub-populations, may reduce the functional population size such that a population becomes more sensitive to demographic stochasticity. One illustrative example of this feature was shown for the Saimaa ringed seal, where the effective population size decreased from 'safe levels' of about 250 to the alarmingly small 6-30 , when the spatial substructure of the 200 Saimaa seals were taken into account (Kokko et al. 1998). On the other hand, spatial subdivision can constitute a protection against random catastrophes since recolonisation of locally extinct colonies can occur from luckier colonies (Harwood and Hall 1990).

During the epizootic in 1988 the harbour seal colonies acted as a host metapopulation for the PDV (Swinton et al. 1998). The distance between sub-populations influenced the spread of the disease (Dietz et al. 1989, Heide-Jørgensen and Härkönen 1992, Swinton et al 1998) and thereby the regional mortality patterns. Remote seal populations, like the small population close to Öland in the Baltic sea, was not infected at all. The spatio-temporal distribution of susceptible seals substantially affect the chances for persistence of an introduced disease. It was found that the PDV in 1988 passed through the European harbour seals and then faded out. Since up to 98% of the seals, in affected areas, was estimated to have been infected by the virus, according to unstructured models (Heide-Jørgensen and Härkönen 1992), the number of susceptibles decreased too fast for the virus to become enzootic (Swinton et al. 1998). Most likely, an outbreak of a similar epidemic in a highly migratory and densely aggregated seal, such as the Baltic grey seal, would have lead to an even more rapid spread of the disease. On the other hand, an epizootic in widely dispersed ice breeding seals, such as crabeater seals and ringed seals, could have difficulties to be established at all during seasons with low contact rate among individuals.

The spatial subdivision of harbour seals is maintained by site-fidelity (IV), which reduces migrations among colonies far below the migratory capacity of individuals. Site-fidelity might be beneficial for an individual for several reasons. One reason might be adjustment to the local breeding time, since harbour seal populations typically have different mean pupping dates on a regional scale (Bigg 1973, Temte et

al. 1991). Alternatively, individuals may simply stay at the place where they were born, since it is likely to be a favourable place to breed. In such a case, local differences in pupping time would not necessarily be adaptive, but just a consequence of local populations 'drifting apart' due to low migration rates. Other factors which vary among local populations due to the spatial substructure are parasite burdens (Lunneryd 1992), environmental toxins (Bernt et al. 1999) and genetic composition (Goodman et al. 1998). To conclude, spatial and temporal structure can potently affect the population dynamics of seals.

An important aspect of spatial and temporal structure within a seal population is the risk for systematic sampling biases, which can create artefactual trends in fertility- and mortality rates and estimates of population growth rate (Thompson et al. 1989, I, III, IV,V). Population growth rate is a basic parameter in modelling of risk assessments and in calculations of harvesting quotas in seals (Wade 1998). The acquisition of fine-scaled data on temporal and spatial distribution can be used to decrease variances of estimates of rates of population increase. Improved estimates of population growth will decrease estimates of extinction risks, and increase recommended harvesting quotas (Engen et al. 1997). Therefore, it is important to not let improved measures of population growth rates lull us into security. Sporadic, catastrophic events that decrease population sizes radically have proven to be an important element in the population dynamics of seals, and their effects are by definition difficult to predict.

The fates of the four species in this thesis illustrate several factors which influence seal populations. The harbour, ringed and grey seals have all been heavily exploited during the last century. One fundamental element is the composition of catches since a hunt directed towards adult females can reduce a population very efficiently. The recovery rates of the three populations differed after hunting was banned. While harbour seals soon reached the theoretically maximum rate of increase the grey and ringed seal populations remained stagnant for decades. Environmental pollution or other factors that cause sterility have profound effects on population growth. The crabeater seal is one of the few seals that has not been subject to large-scale commercial harvest. The strong fluxes in age at sexual maturity and cohort strength indicate that this population can be limited by food availability. The 1988 harbour seal epizootic illustrated how the fine structure of the population interfered with the spread of the disease, and probably influenced the final mortality. Age- and sex-specific behaviour in harbour seals sheds new light on many phenomena, such as variable population growth rates, genetic differentiation and the spread of the epizootic. Fine-scaled spatial and temporal structure of populations can reveal information that is crucial for the understanding of the population dynamics of seals.

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